

## RARITY OF PLANT SPECIES: A SYNTHETIC VIEWPOINT

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Botanists and evolutionists have long been fascinated by species that have narrowly restricted or localized patterns of distribution. Every field botanist can recall the thrill of excitement that comes with the discovery of a new, previously unrecognized species, or of a well known species far outside of its normal range of distribution. In modern times, the preservation of these rarities has become a major concern. This is because they often provide the evolutionist with particularly good opportunities for learning about evolution, in addition to the esthetic pleasure that their very existence provides to countless nature lovers. Learning about them, and about the reasons why they are restricted serves a double function. Such learning is both an avenue toward greater scientific knowledge and a means of increasing the desirability of their preservation.

For more than a century, botanists have theorized and argued about the reasons why some species of plants are rare or local, but no theory has proved altogether satisfactory. This is because the factors involved are numerous and complex. In this article, I shall review some of the theories that have been proposed, and attempt a synthesis to explain the examples known to me.

### HISTORICAL THEORIES

Two well known theories are both based primarily upon knowledge or inferences about the past history of floras. One of these, proposed by J. C. Willis (1922), maintains that most rare species are youngsters that have not had time to spread. The opposite theory, that many rare species are "senescent" and are becoming extinct because of old age, has been promoted by many botanists. In his criticism of Willis, M. L. Fernald (1926, p. 242) stated: "The world not being static, life has followed an almost inextricable series of factors. . .with the result that no single factor, especially *age*, can be isolated as all-controlling" (*italics by Fernald*).

Well documented examples are now available to show that rare and localized species can be either young, ancient, or of an intermediate age. Three hybrid polyploid (amphiploid or allopolyploid) species are known to have arisen less than a century ago: the Town-

send marsh grass, *Spartina townsendii*, (Marchant, 1966); and two species of goatsbeard, *Tragopogon mirus* and *T. miscellus* (Ownbey, 1950). Several localized species, that are either sympatric with or exist close to their nearest relatives, can be inferred on the basis of genetic and distributional evidence to be no more than a few hundred or at most a thousand years old. Among them are *Stephanomeria malheurensis* (Gottlieb, 1973), and *Clarkia lingulata* in the Sierra Nevada of California (Lewis & Roberts, 1956; Gottlieb, 1974).

Several examples of rare or localized species are well known to be ancient and relictual. One of the most renowned of them is the California Big Tree (*Sequoiadendron giganteum*). Well documented evidence shows that its tertiary counterpart was widespread in western North America (Raven & Axelrod, 1977). Fossil evidence also supports the ancient, relictual nature of other modern tree species, such as *Torreya taxifolia* in the southeastern United States, *Metasequoia glyptostroboides* in central China, and *Ginkgo biloba*, a species that is extinct as a wild tree, being known only in cultivation.

One can easily find, in addition, examples of rare species that are neither ancient nor recent. The Monterey Pine (*Pinus radiata*), now confined to three restricted localities along the coast of California, plus Cedros Island off the coast of Baja California, was much more widespread during the Pliocene and Pleistocene epochs (Axelrod, 1967), and so must be regarded as relictual. Nevertheless, it belongs to one of the most advanced sections of the pine genus (Mirev, 1967), and so is not an ancient species compared to other pines. Rare species that on the basis of distributional evidence must be regarded as neither ancient nor very recent include most of those that are being discussed in the present symposium, such as *Geum peckii*, *Potentilla robbinsiana*, and *Pedicularis furbishiae*. Distributional and systematic evidence with respect to most of the rare species known to me causes me to place them in this category. Consequently there appears to be little correlation, either positive or negative, between rarity or localized distributional patterns of species and their chronological age.

#### GENETICAL THEORIES

Most systematic botanists and plant geographers, having long since discarded purely historical theories, have replaced them with theories that emphasize the genetic diversity or homogeneity of their

populations. Depletion or depauperization of the gene pool is often invoked. Such theories were stimulated during the 1930's and 1940's largely by the theories of Sewall Wright (1931), who pointed out that in populations of greatly reduced size, chance fluctuations in gene frequency ("genetic drift") would often lead to fixation of alleles and so to depletion of the gene pool. I theorized along these lines at that time (Stebbins, 1942) but had no good evidence to support my hypothesis. How good are such theories at the present time?

Several rare, endemic species are known to possess very little genetic variability, indicating a much depleted gene pool. A good example is the annual composite, *Stephanomeria malheurensis*, confined to a single locality in eastern Oregon (Gottlieb, 1973). Nevertheless, depleted gene pools are by no means confined to localized endemics. they exist also in widespread species that are largely self-fertilizing (Chapman, 1967). The opposite situation, rare species having relatively rich stores of genetic variability, is also well known. The California Big Tree, *Sequoiadendron giganteum*, has been cultivated in Great Britain for little more than a century, and the majority of trees found there probably were grown from seed collected in the wild. Nevertheless, horticulturists have recognized about twenty-five morphologically recognizable variants among the cultivated specimens that they have grown. This most famous of rare and endemic species appears to contain in its restricted populations nearly or quite as much variability as many common and widespread species. Another example is a rare and localized species of western buckwheat, *Eriogonum apricum*, found in the foothills of California's Sierra Nevada. Although the populations of this species contain hundreds of thousands of individuals, they are confined to a small area of highly sterile soil that is about ten miles long and one to two miles wide. Within each population, differences in leaf form and branching pattern are obvious to the careful observer. In addition, a careful study of morphological variation in neighboring populations has shown that differences between them are great enough so that two different subspecies can be recognized, each of which occupies its own restricted area, the two areas being about five to six miles from each other (Myatt, 1968).

The example of *Eriogonum apricum* needs further investigation, particularly if it turns out to be favorable material for estimating biochemical variability with respect to isozymes. The common,

widespread species, *Eriogonum nudum* occurs sympatrically with *E. apricum*, but on less sterile soils and in company with widespread foothill species. I am willing to predict that a series of populations of *E. nudum* taken from an area equal in extent to that of *E. apricum* will contain no more genetic variability than that present in the totality of populations of *E. apricum*. The widespread distribution of *E. nudum*, in my opinion, is most probably due to the existence of a large number of genetically different populations that are adapted to a wide spectrum of different habitats and climatic zones.

There appears to be no recognizable correlation, either positive or negative, between the amount of genetic variation within populations of plant species and the rarity or commonness of the species as a whole. Other causes for the rarity of species must be sought.

Other theories to explain the occurrence of rare species place great emphasis on ecological factors. Some botanists living in the eastern United States have suggested that rare species are usually pioneers in temporary habitats. Their rarity is then ascribed to the localized occurrence of such habitats and to the possibility that new species can originate in conjunction with the appearance of new and ecologically different pioneer habitats. This hypothesis explains very well the occurrence of several of the endemics discussed in the present symposium. *Geum peckii*, *Potentilla robbinsiana*, *Pedicularis furbishiae*, the New England species of *Astragalus*, as well as the rock plants that inhabit the calcareous cliffs of northern Vermont; all are confined to pioneer habitats. The same is true of the remarkable series of rare species that inhabit the Appalachian shale barrens, the pond margins of Cape Cod, the pine barrens of New Jersey and the major river estuaries along the Atlantic Coast. There are, however, some exceptions, even in the flora of eastern North America. *Shortia galacifolia*, a remarkable endemic of the southern Appalachians, grows under the canopy of climax or subclimax forests. *Prenanthes crepidinea*, one of the rarest species found in the Mississippi Valley, is also an inhabitant of climax forests.

The western United States contains a large number of rare and localized species that, far from being confined to pioneer habitats, form a sort of super climax. The best known of these is *Sequoiadendron giganteum*, but other woody species, such as the Monterey Pine (*Pinus radiata*), Torrey Pine (*Pinus torreyana*), Santa Lucia fir (*Abies bracteata*), and weeping spruce (*Picea breweriana*) are likewise climax or superclimax species. Another feature of the western

flora is the large number of pioneer species that are relatively common and widespread. Nearly all of the species belonging to such large and highly diverse genera as *Astragalus*, *Eriogonum*, *Cryptantha*, and *Penstemon* are pioneers. Many examples exist in the western flora of rare species and their common relatives, both of which are equally well adapted to colonizing pioneer habitats. The predominance of pioneers among the rare species found in mesic areas of relatively low relief, like eastern North America, is due to the comparative rarity of such habitats. In semi-arid regions of the west, where climax forests are often rare and local, species adapted to mesic climax habitats may likewise include a fairly high proportion of rare and endemic taxa.

In discussing the rare and localized species found in California, I have elsewhere (Stebbins, 1976) elaborated on the presence of many of these species on "ecological islands." These "islands" are defined as small areas in which some environmental factor or combination of factors is so different from conditions that prevail in the surrounding areas that with respect to their ability to become established in neighboring areas, the species growing on these "islands" are as isolated as if they were growing on an island in the ocean. Most commonly, the conditions that produce an ecological island are soils of an unusual type. In California, small patches or larger areas of soil derived from ultrabasic or mafic metamorphic rocks, frequently serpentine, form the largest number of ecological islands. Other unusual soils are derived from Tertiary volcanic deposits, such as mud-flow breccia, pumice from recently extinct volcanoes, the sterile soil of raised beaches, and a few localized limestone cliffs in regions that contain predominantly acidic rocks.

While ecological explanations account for most occurrences of rare and localized species, they are no more satisfactory as complete explanations than are any others that rely upon a single factor. For example, they cannot account for the fact that in some instances groups of related species, all of which grow in ecological islands, include some that are narrowly endemic, and others that are widespread. For instance, species of the genus *Streptanthus* or jewel flower (Cruciferae) are among the best known endemics of serpentine barrens in central California. Nevertheless, on these same barrens grow annual species of *Streptanthus* belonging to the same species groups, but relatively widespread. They may consist of similar populations on several different serpentine areas (*Streptanthus*

*breweri*, *S. polygaloides*), or include populations both on and off of the serpentine areas (*S. glandulosus*, Kruckeberg, 1957). Obviously, no strictly ecological theory can explain the differences between these kinds of distributional patterns. Other factors, either different genetical makeup, different past histories, or both must be invoked to explain these differences.

Clearly, the only theories that will provide complete explanations of rarity and endemism of species must be of a synthetic nature. They must take into account ecological factors, genetic structure of populations and past history of the evolutionary lines concerned, and balance these factors among each other in a complementary fashion. A framework for such theories can be a well recognized principle of evolution. This is that rates and directions of evolution may vary greatly, even among related evolutionary lines. The particular rate and direction that will be characteristic of any line will depend upon particular population-environment interactions, mediated by natural selection. I should like to propose a theory based upon this principle, which I am calling the gene pool-niche interaction theory.

According to this theory, the primary cause of localized or endemic distribution patterns is adaptation to a combination of ecological factors that are themselves localized. Factors of soil texture or chemical composition are the most common but by no means the only ones. As pointed out long ago by John Muir, the California Big Tree grows only in parts of the Sierra Nevada that escaped the glacial ice, and are underlain by deep, heavily weathered soils. Nevertheless, *Sequoiadendron* occurs in only a small proportion of these areas. In some instances, temperature and moisture can be recognized as controlling factors, but they do not explain patterns by themselves. For instance, two species of closed cone pines, *Pinus muricata* and *P. radiata*, both occur along the coast of California and are concentrated in areas where summer fog is prevalent, and the mountains do not rise abruptly from the seacoast. The greater tolerance of a cool, rainy winter climate on the part of *P. muricata* as compared to *P. radiata* is evident from its abundance to the north of San Francisco, where *P. radiata* is absent. Nevertheless, *P. muricata* occurs also in south central California, south of the southernmost mainland groves of *P. radiata*, and in a milder, drier climate. This anomaly is probably explained by the genetic structure and past history of the two species. Evidence from artificial hybridi-

zation suggests that *Pinus muricata* as recognized in the floras actually consists of two species, the more southerly of which occurs south of the mainland localities for *Pinus radiata* (Critchfield, 1967). The more southern or typical *P. muricata*, moreover, appears to be closely related to and apparently descended at least partly from a series of populations once described as *P. remorata*, which were apparently adapted to a relatively mild climate (Axelrod, 1967).

Next to climatic and edaphic factors, those inherent in the gene pool of the population are of critical importance. They include the total amount of variability, the amount of variability that can be released at any one time, and the amount of variation that can be generated with respect to those particular characteristics that affect most strongly the establishment of new populations. Prominent among the latter are seed production, the distance to which seeds can be dispersed, as well as seed size and other characters that aid in the establishment of seedlings.

A good example of the effect of the nature of seed dispersal mechanisms upon rare or endemic vs. widespread distribution of species is the contrast between the distribution of species of juniper (*Juniperus*) and cypress (*Cupressus*) in the western United States. These related genera form trees or large shrubs having very similar vegetative characteristics. They are both wind pollinated and form seeds approximately similar in size. Both genera include species adapted to arid habitats, and others that are more mesic. The most conspicuous difference between them is that the seeds of *Cupressus* are borne in hard, woody cones, from which they drop to the ground when ripe, while those of *Juniperus* are borne in berries that are eaten by birds, which excrete them at considerable distances from the parental tree. It is no accident, therefore, that species of *Juniperus* are all widespread, some of them extremely so, while *Cupressus* contains a higher proportion of localized species than any other woody genus of North America.

One way in which an impression can be gained of the ways in which these factors interact is to visualize the niche as a depression that is partly filled by a liquid, the gene pool. Ecological islands such as serpentine barrens surrounded by large areas of acidic soils would then be deep, narrow depressions. If the "pool" should occupy such a depression, its store of variability would be represented by the depth of the liquid. Since even a relatively deep "pool" would have a

surface far below the rim of the depression (i.e. even the most extreme variants that a rich gene pool could generate would fall far short of adaptation to the surrounding area), the size of the gene pool would in this case affect relatively little the ability of the species to colonize new areas and expand its range. Ecological islands based upon more subtle environmental factors, such as those that apparently affect the distribution of species like the giant Sequoia and the Monterey Pine, can be visualized as relatively shallow depressions. In these examples, a species having a restricted gene pool can be likened to a thin film of liquid at the bottom of the depression, from which few or no droplets can rise and spread to neighbouring depressions. Species having larger gene pools fill the depression more completely, so that their restriction does not depend upon a simple kind of population-environment interaction that keeps them in place. Their restriction is due either to low vagility, usually conditioned by seeds having poor dispersability or difficulty of establishment, to a great distance that separates one favorable niche or depression from another, or to a combination of these and other factors.

Like every other problem of evolution, that of the nature and occurrence of rare species is not a simple one that can be solved by applying indiscriminately one or a few general principles. Each example of such species has its unique features, and must be considered with respect to three major parameters: the intricate mosaic of the environment in which it grows; the complex genetic structure of its populations, including the amount and nature of genetic variability, as well as the way in which it becomes revealed and exposed to natural selection; and finally the past history of the populations, that may provide a clue to understanding why a particular genetic structure and environment-population interaction exists. The problem of the evolution and persistence of rare and endemic species is merely one facet of the much larger problem of biological evolution in general. The synthetic method is the only rational approach to all evolutionary problems.

The very fact that problems posed by the occurrence of rare and endemic species are isolated facets of evolutionary problems in general confers on such species a particular importance. As already recognized half a century ago by Fernald (1926), a full understanding of their nature and origin can give us particular insight into rates



and directions of evolution. To the dedicated naturalist, the thrill of discovering or rediscovering these priceless rarities can be matched by the succession of pleasures and satisfactions that accompany unravelling, step by step, the mysteries of their origin. Whenever one of them becomes extinct, future generations of naturalists are deprived of one more chance to experience these thrills and pleasures while adding to mankind's knowledge about the world in which we live.

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